HYBRIDIZATION OF RUBUS HISPIDUS AND R. SETOSUS[1]

FREDERIC STEELE AND A. R. HODGDON

In an earlier paper (Hodgdon and Steele 1962) it was pointed out that *Rubus allegheniensis* is highly variable in its glandularity thus casting doubt on the validity of using the presence or absence of glands on the primocane as a character to separate species in the Section *Alleghenienses*. It is presumed that this and other characters such as the nature of the inflorescence, shape of leaf or leaflet, amount of pubescence, etc., may show a similar degree of intraspecific variability in many species of the Subgenus *Eubatus*. Part of the taxonomic confusion in the blackberries undoubtedly has resulted from the failure of students to appreciate the range of variability in the better known and more widely distributed species.

An added dimension of variation in *Rubus* Subgenus *Eubatus* is produced by hybridization. With reference to crossing in the group, Bailey (1941) presented a singularly critical commentary on those taxonomists such as Rydberg, Brainerd and Bicknell who had postulated or accepted hybridity as an important factor in the American blackberries. Bailey was unwilling to accept hybridization as of importance in the group, for he stated (p. 7) "It is to be noted that even after all these years of assumption of miscellaneous crossing in the American brambles we do not yet have a satisfactory demonstration of the problem in nature . . ." and later on, "one may find in the field what are apparently real hybrids but they appear to be no more common or any more puzzling than in other large genera; and in such cases a scrap on an herbarium sheet would not be evidence.

The hybridity postulate cannot explain the pomological blackberries."

In order to understand Bailey's thinking about Rubus better it may be well to quote further. Toward the end of page

[1]Published with approval of the Director of the New Hampshire Agricultural Experiment Station as Scientific Contribution No. 314.

7 he gave the following criteria for recognizing hybrids, "(1) the presence of the two parents in the vicinity; (2) occurrence usually in small numbers, as if incidental or exceptional to the main population; (3) characters that appear to belong only to the parents in various degrees of combination."

From the context in which he wrote, it is evident that Bailey's rejection of hybridity was a reaction to the common but unfortunate taxonomic practice of calling plants hybrids without sufficient evidence, but his thinking about hybrids is hardly acceptable as a generalization in the light of present knowledge. Hybridization between species may occur infrequently or not at all in many groups, although it is a frequent process in many genera and it is certainly common in *Rubus* Section *Eubatus* in which hybrids may be found between many of the common well-known species whenever these occur together in some abundance in disturbed areas.

Fernald (1950) had quite accepted hybridization in the blackberries. But it is one thing to accept hybridization as an operating mechanism in a group and another to apply it successfully in working up the taxonomy of that particular group. Fernald's procedure in the Manual was to retain all but the most obviously overlapping taxa. He would have had to be highly arbitrary to do otherwise for all of the hundreds of "species" that had been described were set apart on the basis of supposed morphological differences that seemed to make each distinct and in the majority of cases there was no available information to show that one was any better as a species than another. He did perform the valuable service of eliminating a very large number of very dubious taxa in the group. Because he did retain those taxa which he believed to be most distinct morphologically, his treatment does provide an excellent point of departure for further work. In the "Manual" therefore is to be found the nucleus of any sound taxonomic study of blackberries in Northeastern America.

Gleason & Cronquist (1963) have accepted the fact that

hybrids are common in blackberries; they have also reduced the number to a very few and at times arbitrarily selected "collective species" some of which are too broad to represent biological realities and others are trivial and based on inconsistent distinctions. While attractive to the non-specialist who wants to give some name to his collections, their treatment does have shortcomings. If an enormous assemblage of taxa is to be reduced to few, it is only by an intensive and specialized approach that the accurate dilineation of all the basic species can be accomplished.

This paper presents evidence that hybrid and introgressing populations between 2 species of *Rubus* Section *Eubatus* do occur rather frequently and further that three widely recognized, so-called, species exhibit taxonomic characteristics that are shared by various of these evident hybrids. Thus perhaps for the first time we present evidence from field studies that hybridization is an important factor in blackberry taxonomy.

Quite early Brainerd and Peiterson (1920) suggested hybridization as an important factor in the Rubus problem, and proposed a rather elaborate scheme of hybrids. Although they made a number of collections and did some experimental work, they published no direct evidence of hybridization and their results were not accepted by Bailey or Fernald. Nevertheless an examination of specimens in the Pringle Herbarium at the University of Vermont has convinced us that some of Brainerd and Peiterson's conclusions were valid. However, each supposed hybrid must be considered separately and appropriate tests applied. We have used the following criteria for hybridization: 1. that the putative parents be present in the area; 2. that the supposed hybrids occupy a disturbed environment; 3. that the supposed hybrids show some degree of intermediacy between the two parents. Blackberries frequently grow in disturbed environments, such as gravelly edges of roads or lumbered areas so condition 2 is easily satisfied. It was realized that many of the populations would show introgression with one of the parents.

Although we have similar evidence that many species of *Rubus* hybridize, this paper will be concerned with *R. hispidus* and *R. setosus*. *R. hispidus* is typically a blackberry of dry, open, or shady habitats with rather poor soil. It also grows in boggy areas. It is most easily recognized by its prostrate habit, lack of sharp prickles, and three lustrous coriaceous primocane leaflets. *R. setosus* is typically an inhabitant of alluvial meadows and poorly drained soil, but will grow in a variety of open habitats. It is a low erect blackberry with numerous soft bristles and poor fruit.

The first indication that these species might hybridize arose when the senior author noticed a mongrel population of blackberries along the gravelly edge of a newly constructed state road. A number of clones were scattered in the bare gravel, each somewhat different from the others, and all clearly having existed for only two years. Both *R. hispidus* and *R. setosus* grew in the area so it seemed quite possible that this was a hybrid population. Collections were made and investigations started on the possibility of frequent hybridization and introgression of these two species.

To analyze the situation it was decided to use the hybrid index method as described by Stebbins (1950). For each colony of blackberries investigated, 8 plants, consisting of both primocane and floricane from the same rootstock were collected. Each plant was tagged at the time of collection with data as to the growth habit. It was noticed that new primocanes often started off as erect plants, and may not have developed trailing tendencies until after flowering time so no collections were made until after the first of July. In the case of a long primocane, the midportion with leaves that seemed to be typical of the whole plant were secured; for the floricane, care was taken to secure a vigorous branch of the inflorescence with remains of flowers. Fruits often do not develop. Samples were taken from the colony at regular intervals in the case of a roadside population, or else in such a way as to indicate the range of variation.

In the preparation of the index all characters except growth habit were rated 0, 1 or 2.

TAXONOMIC CHARACTERS USED IN STUDY

GROWTH HABIT — varies from prostrate through low and high doming, to erect. This is an excellent character and it was rated from 0 to 4. Good *R. hispidus* is always prostrate, but in certain situations may trail on vegetation to some height above the ground. Floricanes of *R. setosus* are often reclining or lodged because of the weight of snow; if the primocane is erect the plant is considered erect. It should be emphasized that growth habit can only be accurately rated if notes are made at time of collection. A number of otherwise excellent herbarium specimens lack this essential data.

ARMATURE PER DECIMETER — a good character but somewhat subject to environmental modification. The count included prickles, bristles, and glands. Although *R. setosus* typically has a large number of bristles, they may be quite sparse near the base of the stem; their number is also affected by shade.

LENGTH OF THE LONGER BRISTLES — runs from .25 cm. or less for *R. hispidus* to .4 cm. or greater for *R. setosus*. It is not always consistent.

CHARACTER OF PRIMOCANE LEAF — *R. hispidus* coriaceous and lustrous under good light; *R. setosus* dull and chartaceous.

NUMBER OF PRIMOCANE LEAFLETS — *R. hispidus* typically 3; *R. setosus* 5 or sometimes 3 with 2 of them partly divided.

LENGTH OF CENTRAL PRIMOCANE LEAFLET — *R. hispidus* noticeably smaller, usually less than 5 cm.; *R. setosus* 6.5 cm. to 11 cm. This character is subject to some environmental modification.

Position of broadest part of leaf was expressed as the ratio of the distance of the broadest part of the leaf to the center of the leaf divided by half the length. This ratio varies from .1 to .3 for *R. hispidus;* thus the leaves tend to be obovate. In *R. setosus* the ratio is usually 0 with leaflets broadest at the middle.

CHARACTER OF TEETH OF LEAFLET — *R. hispidus* has teeth rounded with an abrupt point; *R. setosus* has teeth triangular or accuminate.

LEAF TIP OF CENTRAL PRIMOCANE LEAFLET — *R. hispidus* is usually rounded and abruptly pointed; *R. setosus* typically has an accuminate tip.

DIAMETER OF PRIMOCANE — *R. hispidus* 2mm. or less; *R. setosus* usually 3 mm. or more but occasionally less in shady situations.

GLANDULARITY OF FLORAL AXIS — *R. hispidus* has either no glands or rather sparse glands of uniform length; *R. setosus* has abundant glands of varying length.

Table I. List of characteristics used in Hybrid index with values assigned.

	R. hispidus		*R. setosus*
Growth habit	Prostrate = 0	Doming = 2	Arching to erect = 4
Armature per dm.	0-2000 = 0	2001-2999 = 1	3000 or more = 2
Bristle length	3 mm. or less = 0	3.1-3.9 = 1	4 mm. or more = 2
Character of leaf	Lustrous coriaceous = 0	Intermediate = 1	Dull Chartaceous = 2
No. primocane leaflets	3 = 0	3-5 = 1	5 = 2
Length of leaflet	0-5 cm. = 0	5-6.5 = 1	6.5 or more = 2
Mid ratio	.3-.1 = 0	——	0 = 2
Teeth	*R. hispidus* type = 0	Intermediate = 1	*R. setosus* type = 2
Tip of leaflet	Abruptly pointed = 0	——	Acuminate = 2
Stem-diameter	2 mm. = 0	——	3 mm. or more = 2
Glands in infl.	0-few = 0	——	Abundant = 2

Discussion

In order to provide standard material for effective comparisons, we made collections from characteristic *Rubus hispidus* and *R. setosus* colonies. The results of the analysis of these collections provide the information about the two species shown in figure 1. A total of 11 hybrid or introgressing populations were analyzed of which only 6 could be shown in the diagram. In general these were chosen to show the range of intermediacy in these populations. It is

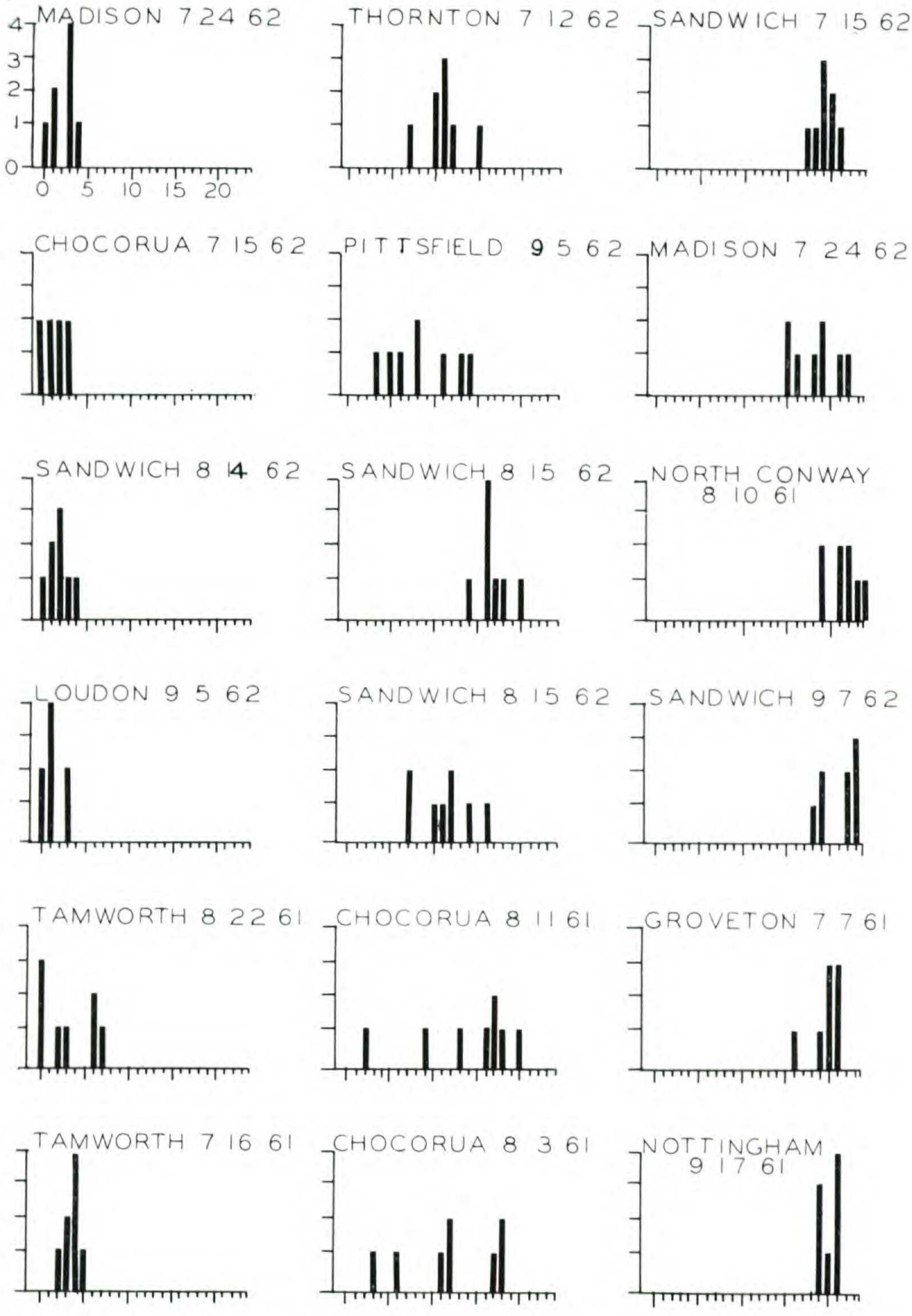

Figure 1. Frequency Distribution Diagram: *Rubus hispidus* populations at left. *R. hispidus* × *R. setosus* in center and *R. setosus* at right. The hybrid index values are on the horizontal axis, the numbers of individuals measured on the vertical axis (scale given in upper left of diagram).

to be noted that in some of the populations certain plants may grade into one or both parents though the majority fall into a position between them. The limit of anything we would tend to call *R. hispidus* would be not more than 7 in value while *R. setosus* would be not less than 16 on the scale.

During this investigation it has become apparent that several controversial "species" are hybrids or introgressants intermediate in character between *Rubus hispidus* and *R. setosus*. Those most clearly intermediate are *R. adjacens* Fernald, *R. jacens* Blanchard and *R. trifrons* Blanchard. Two others, *R. spiculosis* Fernald and *R. tholiformis* Fernald display many intermediate features and may belong in this category or may have a more complicated heredity.

In the folders of *R. adjacens* in the Harvard Herbaria one finds a varied assortment of material varying from specimens close to *R. setosus* to strongly intermediate plants. The same in general holds true for *R. jacens* while *R. trifrons* has more frequently been confused with *R. hispidus*. To lend clarity to this problem we have investigated the type specimens of these three and have graded each according to our hybrid index values. Although information is lacking about the habit of growth of the type of *R. trifrons*, it is possible nonetheless, to get a fairly good idea of the probable relationship of these three from the total values. The hybrid index value of 11 for *R. adjacens* shows it to be clearly intermediate between *R. hispidus* and *R. setosus* as does the value of 10 for *R. jacens*. *R. trifrons*, as might be suspected from its frequent confusion with *R. hispidus*, has a slightly lower value of 9.

We conclude that hybridization and introgression of *R. hispidus* and *R. setosus* occur frequently especially in disturbed areas giving rise, in addition to the above mentioned recognized taxa, to various other forms difficult to classify.

We wish to thank the curators of the Gray Herbarium, the Arnold Arboretum Herbarium and that of the New England Botanical Club for permission to examine their collections of Rubus. We also extend thanks to Dr. H. W. Vogelmann and L. Charette for the loan of specimens and

for permitting us to examine the Rubus collections in the Pringle Herbarium at the University of Vermont.

Voucher specimens are deposited in the herbarium of the University of New Hampshire.

ST. MARY'S-IN-THE-MOUNTAINS, LITTLETON, NEW HAMPSHIRE, AND UNIVERSITY OF NEW HAMPSHIRE, DURHAM.

Literature Cited

BAILEY, L. H. 1941. Species Batorum. The Genus *Rubus* in North America. Gent. Herb. **5**: 6-8.

BRAINERD, EZRA and A. K. PEITERSEN. 1920. Blackberries of New England — Their classification. Vt. Ag. Exp. Sta. Bull. 217: 84 p.

FERNALD, M. L. 1950. Grays New Manual of Botany, 8th ed. New York: 822.

GLEASON, H. A. and ARTHUR CRONQUIST. 1963. Manual of Vascular Plants. Princeton, N. J.: 810 p.

HODGDON, A. R. and FREDERIC STEELE. 1962. Glandularity in *Rubus Allegheniensis* Porter. Rhodora **64**: 161-168.

STEBBINS, G. L. 1950. Variation and Evolution in Plants. Columbia: 265-270.